

DARWIN FORMATION (EARLY CRETACEOUS, NORTHERN TERRITORY) MARINE REPTILE REMAINS IN THE SOUTH AUSTRALIAN MUSEUM

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Marine reptile remains from Early Cretaceous (Aptian/Albian) deposits of the Darwin Formation, Northern Territory, are described from the collections of the South Australian Museum. The material includes vertebra and limb girdle elements from ichthyosaurs and plesiosauroids, as well as the first described pliosaurid remains from the Northern Territory. The pliosaurid specimen (a single femur) is attributed to the small-bodied (up to 3 m in length) freshwater/near-shore marine taxon *Leptocleidus*, supporting interpretation of the Darwin Formation as representing a near-shore marine depositional environment. A comparison of the Darwin Formation marine reptile fauna with those known from Early Cretaceous deposits elsewhere in Australia, indicates greatest compositional similarity to the Hauterivian–Barremian Birdrong Sandstone fauna of Western Australia. A potential link between the distribution of some marine reptile taxa (eg pliosaurids) and the prevailing depositional environment is also suggested.

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Sometime in the 1960s (exact date unknown), a small collection of fossil marine reptile remains from the Early Cretaceous (Aptian/Albian) deposits of Casuarina Beach, Darwin Formation, Northern Territory (see Murray 1987, Fig. 1, p. 95 for locality map) was donated to the South Australian Museum. In 1994 several additional Darwin Formation marine reptile specimens were acquired as part of an exchange with the Museum and Art Gallery of the Northern Territory. A recent examination of these remains, which include isolated elements from both ichthyosaurs and plesiosauroids, has also revealed the presence of a pliosaurid femur. This specimen is attributable to the genus *Leptocleidus* Andrews, 1922 and represents the first documented pliosaur material from the Northern Territory. This paper describes Darwin Formation marine reptile remains currently housed in the South Australian Museum and provides a brief palaeoecological analysis based on faunal comparison with other known Early Cretaceous marine reptile bearing deposits.

Marine reptile remains were first reported from the Darwin Formation by an anonymous author (1924) who described a fragmentary ichthyosaur skeleton from Fannie Bay near Darwin. This specimen was later attributed to *Ichthyosaurus australis* (Tiechert & Matheson 1944); however,

Murray (1985) re-assigned the material, along with other ichthyosaur remains from Nightcliff, north of Fannie Bay, to *Ichthyosauria* gen. et sp. indet. A more recent examination by Wade (1990) suggested that all ichthyosaur material from the Darwin Formation might be synonymous with *Platypterygius longmani* from the Aptian–Albian of Queensland. Murray (1987) described isolated ichthyosaur and elasmosaurid remains from Casuarina Beach, assigning the material to *Platypterygius* sp. and *Elasmosauridae* gen. et sp. indet., respectively. The presence of elasmosaurid and pliosaurid remains in the Casuarina Beach deposits was also noted by Cruickshank et al. (1999) but no descriptions were provided.

A comparison of the Darwin Formation marine reptile fauna with those known from Early Cretaceous deltaic-marine deposits elsewhere in Australia (Wallumbilla Formation [Doncaster Member], Allaru Mudstone, Toolebuc Formation and Mackunda Formation, Queensland; Bulldog Shale, South Australia; Wallumbilla Formation [Doncaster Member], New South Wales; Birdrong Sandstone and Barrow Group, Western Australia) indicates greatest compositional similarity to the Hauterivian–Barremian Birdrong Sandstone fauna, with ichthyosaurs, elasmosaurids and the small-bodied pliosaurid *Leptocleidus* represented. A potential link between the distribution of some

marine reptile taxa (eg pliosaurids) and the prevailing depositional environment is also suggested. The presence of *Leptocleidus*, a pliosaurid genus known otherwise from freshwater and near-shore marine deposits (Andrews 1911, 1922; Strömer 1935; Cruickshank 1997; Cruickshank & Long 1997; Cruickshank et al. 1999) supports interpretation of the Darwin Formation as representing a shallow near-shore marine depositional environment (*sensu* Smart & Senior 1980; Murray 1985; Henderson 1998).

MATERIALS AND METHODS

Institutional abbreviations used: SAM, South Australian Museum, Adelaide; NTM, Museum and Art Gallery of the Northern Territory, Darwin; AM, Australian Museum, Sydney.

Lithostratigraphic nomenclature follows Mory (1988) for Early Cretaceous deposits of the Darwin area and Burton & Mason (1998) for the opal-bearing sediments of White Cliffs, New South Wales. Systematic terminology follows Montani (1999) for Ichthyopterygia and Brown (1981) for Plesiosauria except in the subdivision of Pliosauroida, in which Polycotylidae is retained as a separate family (*sensu* Williston 1925; White 1940; Persson 1963; Welles 1962; Carpenter 1996, 1997). Functional sub-division of the vertebral column in ichthyopterygians follows Buchholtz (2001), with designation of structural units as neck, trunk, tail stock and fluke. Interpretation of plesiosaur pelvic and femoral musculature follows Robinson (1975) and Lingham-Soliar (2000). All measurements were taken using callipers and are in millimetres (mm).

GEOLOGICAL SETTING AND PRESERVATION

The marine reptile-bearing deposits of the Darwin Formation are typically characterised by glauconitic sandstone and radiolarian mudstone with basal quartzose conglomerate and localised nodular phosphorite horizons (Henderson 1998). The unit forms part of the Bathurst Island Group, which rests nonconformably on Precambrian basement within the Money Shoals Platform (see Fig. 1, p. 117 and Fig. 6, p. 124 of Henderson 1998 for locality and stratigraphic setting). At its base, the Bathurst Island Group is composed of the laterally equivalent Darwin Formation and Marligar Formation, which are overlain in turn by the Wangarlu Mudstone and Moonkinu

Formation.

The Darwin Formation has historically been considered Albian in age on the basis of its macroinvertebrate (Day 1969; Skwarko 1966, 1968; Henderson 1990) and palynomorph (Morgan 1980) assemblages; however, more recent analyses (Henderson 1998; D. Megirian pers. comm. 2000) suggest an upper Aptian age. The Marligar Formation has been dated as Neocomian/Aptian by palynological studies (Burger 1978) and upper Aptian because of its laterally equivalent relationship with the Darwin Formation (Henderson 1998). The overlying Wangarlu Mudstone is regarded as upper Albian–Cenomanian (possibly with a basal lower Albian component, Henderson 1998) on the basis of ammonite (Henderson 1990) and palynological (Norvick & Burger 1975; Burger 1978) data. The uppermost Moonkinu Formation is considered Cenomanian–Turonian on account of its ammonite (Wright 1963) and bivalve/gastropod/scaphopod (Skwarko 1983) faunas.

The glauconitic sandstones and predominant radiolarian mudstones of the Darwin Formation reflect a near-shore marine/paralic depositional environment (Smart & Senior 1980; Henderson 1998). The presence of a limited benthic invertebrate fauna also suggests unfavourable, possibly anoxic bottom conditions (Henderson 1998).

The Darwin Formation marine reptile remains generally occur as heavily weathered isolated elements, although several fragmentary skeletons have been recovered (Murray 1985; D. Megirian pers. comm. 2000). The disarticulated nature of the remains led Murray (1985) to speculate that an inshore and/or tidal depositional environment may have facilitated stranding of decaying carcasses on mudflats prior to burial.

SYSTEMATICS

DIAPSIDA Osborn, 1903

ICHTHYOPTERYGIA Owen, 1860

ICHTHYOSAURIA de Blainville, 1835

OPHTHALMOSAURIA Appleby, 1956 (*sensu* Montani 1999)

Platypterygius von Huene, 1922

cf. Platypterygius longmani

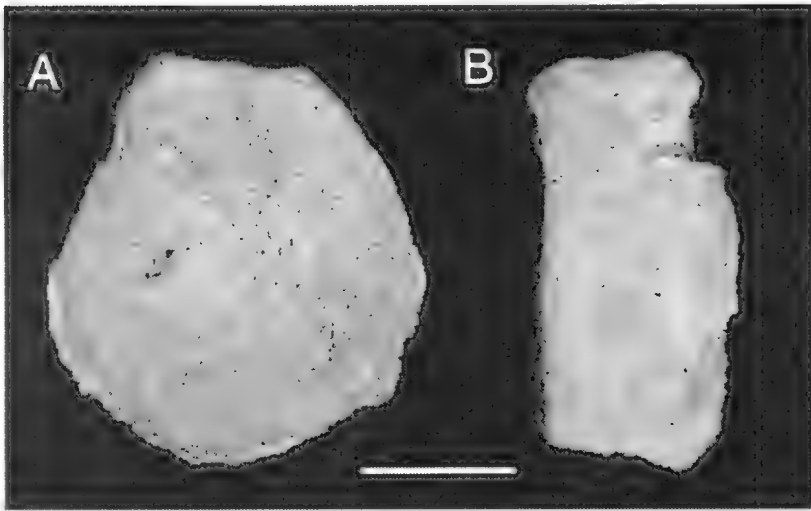


FIGURE 1. SAM P35039, *cf. Platpterygius longmani* dorsal vertebra in (A) anterior and (B) lateral views. Scale bar is 40 mm.

Material

SAM P35039 (Figs 1A, B; Table 1), four associated mid-posterior trunk vertebral centra; SAM P35426 (Table 1), two articulated anterior

trunk centra; SAM P35427 (Table 1), three associated anterior tail stock centra; SAM P35429 (Table 1), two associated sections of eight and four articulated anterior? tail stock centra; SAM

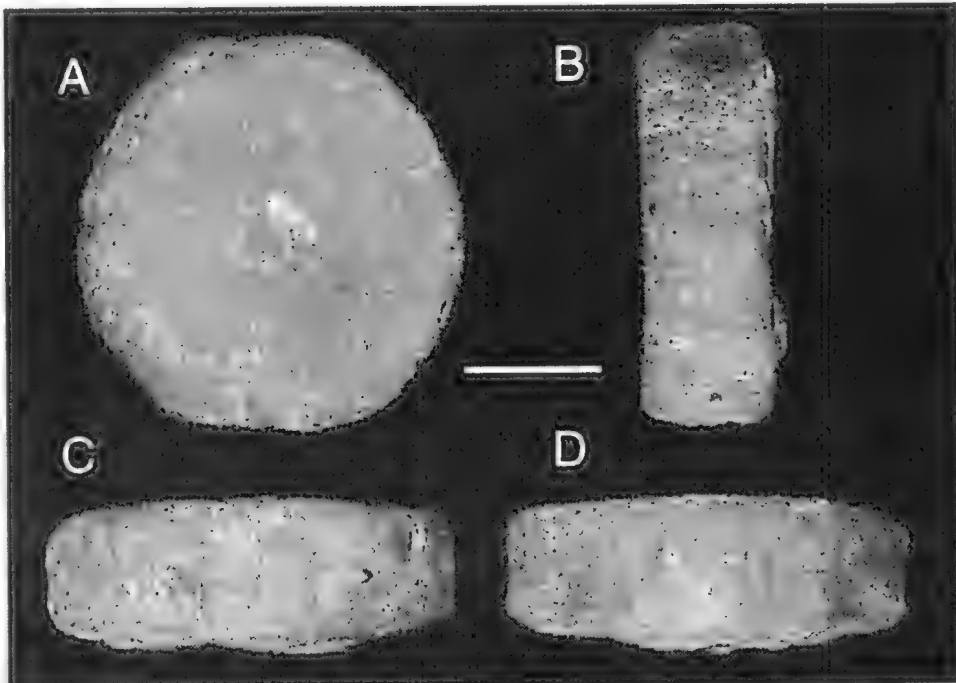


FIGURE 2. SAM P35430, *cf. Platpterygius longmani* caudal vertebra in (A) anterior, (B) lateral, (C) ventral and (D) dorsal views. Scale bar is 20 mm.

TABLE 1. Measurements (mm) of *cf. Platypterygius longmani* vertebral centra from the Darwin Formation, Northern Territory.

| Specimen | Length | Width | Height |
|-------------|--------|-------|--------|
| SAM P35039 | 39.6 | 91.2 | 98.9 |
| | 33.1 | 88.9 | 90.2 |
| | 30.2 | 80.1 | 89.2 |
| | 32.3 | 62.6 | 66.1 |
| SAM P35426 | 40.6 | 85.5 | 88.9 |
| | 37.0 | 86.1 | 89.7 |
| SAM P35427 | 40.7 | 94.0 | 96.4 |
| | 30.1 | 86.2 | 92.4 |
| | 25.8 | 102.8 | 109.6 |
| *SAM P35429 | 24.9 | 81.6 | 69.9 |
| | 25.8 | 83.1 | 75.2 |
| | 26.4 | 86.4 | 79.1 |
| | 25.2 | 64.8 | 83.9 |
| | 20.5 | — | 78.2 |
| | 21.6 | 58.3 | 60.1 |
| | 21.1 | 58.9 | 50.8 |
| | 22.3 | — | 57.2 |
| | 17.4 | — | 55.1 |
| | 18.9 | — | 46.6 |
| | 14.1 | — | 46.9 |
| — | — | — | |
| SAM P35430 | 20.8 | 68.9 | 59.7 |
| | 20.8 | 61.1 | 62.1 |
| | 18.7 | 55.7 | 56.1 |
| | 14.6 | 53.2 | 50.4 |
| | 15.3 | 47.9 | 48.3 |
| | 15.3 | 42.8 | 42.6 |
| | 15.2 | 43.6 | 45.0 |
| | 12.9 | 41.5 | 41.3 |

* some centra represented by fragments only

P35430 (Figs 2A, B, C, D; Table 1), nine associated anterior tail stock centra (juvenile).

Locality

Casuarina Beach, north of Darwin, Northern Territory. Darwin Formation, Aptian or Albian.

Description

All of the preserved centra are disc-like and anteroposteriorly compressed, with the dorsal length subequal to the ventral. Tail stock centra (Figs 2A, B, C, D) exhibit a more marked degree of anteroposterior compression relative to those from the trunk region (Figs 1A, B) and are slightly

ovoid in outline, with height being approximately 1.5 times the transverse width. The articular surfaces of all centra are deeply amphicoelous, with a distinct central notochordal pit. The neural canal is generally broad and shallow, becoming narrower in centra from the tail stock region. The neural arch facets are narrow and rectangular in all centra. Where preserved, both the diapophyses and parapophyses of the trunk centra are distinctly raised and subcircular. This is unlike centra from the tail stock region, in which only the ovoid diapophysis is present and positioned low on the lateral centrum surface. The ventral surfaces of at least two of the recovered centra from the tail stock region show distinct haemal arch facets. These are slightly concave and saddle-shaped in outline with low ridge-like margins. Medially, the haemal arch facets border the very weakly concave, spool-shaped depression for the haemal canal.

Remarks

All of the ichthyosaur vertebral centra examined can be distinguished from those of basal ichthyopterygians by their disc-like shape and strong anteroposterior compression (the more plesiomorphic Grippidia having cylindrical centra, Montani 1999). The absence of any further diagnostic features restricts attribution of the specimens to Ichthyosauria gen. et sp. indet. However, tentative assignment of the remains to *cf. Platypterygius longmani* is justifiable on the basis of: 1) overall similarity to *P. longmani* vertebral material described from the Allaru Mudstone and Toolebuc Formation, Queensland (Wade 1990) and Darwin Formation (Murray 1985, 1987 *sensu* Wade 1990); and 2) current recognition of *P. longmani* as the only valid ichthyosaur species from the Aptian–Albian of Australia (Wade 1990; Bardet et al. 1994; Arkhangelsky 1998; Montani 1999).

Buchholtz (2001) discussed differentiation of structural units within the vertebral column of Jurassic ichthyosaurs with relation to variation in swimming styles between taxa. Following on from this study, it can be suggested that differences observed in the Darwin Formation centra (relating to regionalised morphological variation along the vertebral column) can be used to predict preferred swimming style in the Cretaceous *P. longmani*. The marked increase in height proportionate to width, and anteroposterior compression of the tail stock relative to trunk centra, in the Darwin Formation specimens is comparable to the condition recorded in derived thunniform-model

ichthyosaurs such as *Ophthalmosaurus icenicus* and *Stenopterygius quadrissicus* (Buchholtz 2001). Wade (1990) and Broili (1907) noted that the anterior fluke centra in *P. longmani* and *P. platydactylus* were distinctly higher than wide, a feature also conforming to the predicted thunniform condition. Taken together therefore, these characteristics may suggest that *Platypterygius* spp. employed an axial oscillatory swimming mode and probably shared many other key traits (see Montani 1999; Buchholtz 2001) with derived thunniform-model ichthyosaurs.

SAUROPTERYGIA Owen, 1860

PLESIOSAURIA de Blainville, 1835

PLESIOSAUROIDEA (Gray, 1825) Welles, 1943

Plesiosauroida gen. et sp. indet.

Material

SAM P35431 (Figs 3A, B, C), incomplete and badly weathered element tentatively identified as the ventral plate portion of a left ischium. Orientation is based on position of the lateral margin and its attitude relative to the horizontal axis; SAM P35434 (Figs 4A, B, C), right ischium lacking part of anteromedial margin.

Locality

Casuarina Beach, north of Darwin, Northern Territory. Darwin Formation, Aptian or Albian.

Description

Dimensions of remains are: SAM P35431, total length of 96.7 mm; total width is 98.9 mm; maximum height is lateral extremity is 22.5 mm; maximum length of lateral extremity is 55.3 mm; maximum height of ventral plate is 45.9 mm. SAM P35434, total length is 74.6 mm; total width

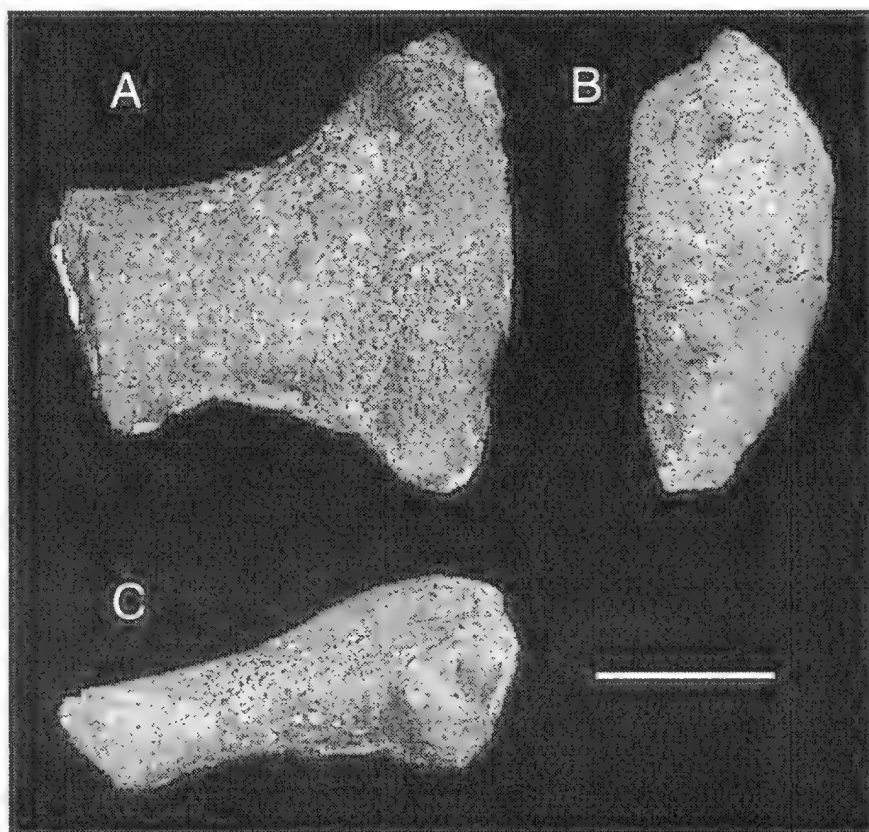


FIGURE 3. SAM P35431, *Plesiosauroida* gen. et sp. indet. partial ischium in (A) dorsal, (B) medial and (C) posterior views. Scale bar is 40 mm.

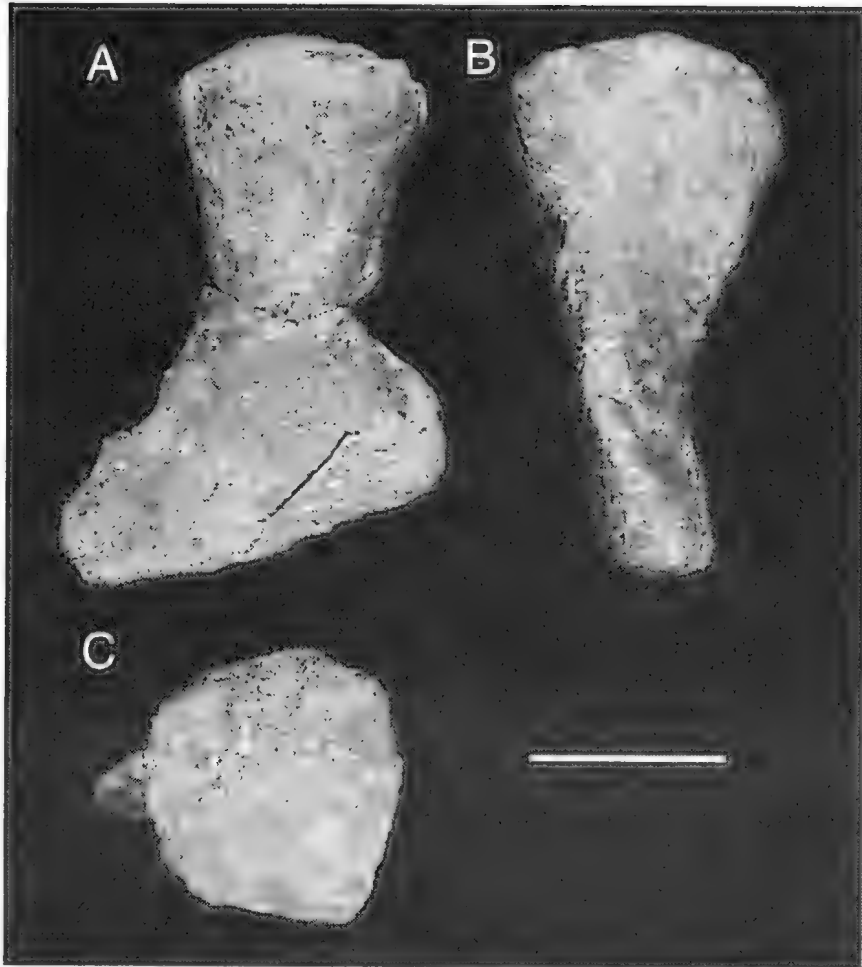


FIGURE 4. SAM P35434, Plesiosauroidea gen. et sp. indet. ischium in (A) dorsal, (B) posterior and (C) lateral views. Scale bar is 40 mm.

is 97.4 mm; maximum height of the of lateral articular surface is 52.1 mm; maximum length of lateral articular surface is 46.1 mm; maximum height of ventral plate is 10.8 mm. Both SAM P35431 and SAM P35434 are hatchet-shaped in dorsal outline with an anteroposteriorly expanded ventral plate. The lateral articular extremity of SAM P35434 is massive but has been lost in SAM P35431. Medially, the ventral plate portion of both elements is dorsoventrally compressed with an inclined medial edge for contact with the opposing ischium. This surface is oriented approximately 10° ventral to a horizontal plane through the lateral articular extremity, and is deeply pitted, suggesting the presence of cartilage. Both the dorsal and ventral surfaces of the ventral

plate in SAM P35434 are rugose, possibly for attachment of the m. puboischiofemoralis internus and m. p. externus, respectively. A weak ridge on the posteromedial margin of the ventral plate may also have supported slips of the m. ischiotrochantericus. The ventral plate of both specimens is not greatly anteroposteriorly expanded (with total length being just slightly less than the total transverse width of each element) and is separated from the lateral articular extremity by a constricted waist-like midsection. This is ovoid to circular in cross-section, becoming increasingly dorsoventrally thickened towards the lateral articular surface (not preserved in SAM P35431). The articular surface itself is convex, with the rectangular anterior pubis facet

offset approximately 195° relative to the longitudinal axis of the articular surface. The pubis facet is separated posteriorly from the rectangular median acetabular facet, and in turn from the lobate posterior-most ilial facet (offset approximately 150° relative to the longitudinal axis of the articular surface) by weak parallel ridges. The articular surface margin is produced into a crenate rim, which is continuous ventrally, with a low rugose tuberosity possibly marking part of the *m. puboischiofemoralis internus* attachment.

Remarks

Despite being heavily weathered, SAM P35431 is identified as the ventral plate portion of a plesiosaurian left ischium on the basis of its hatchet-shaped outline and general morphology. Nevertheless, the specimen is unusual in its markedly dorsoventrally deep, medial articular margin. SAM P35431 was initially registered as an ichthyosaurian humerus belonging to *Platypterygius* sp. However, such an identification is unlikely as the humeri of *Platypterygius* spp. are much more robust, with rectangular to spool-shaped dorsal outline and prominent ridge-like tuberosities on both the dorsal and ventral surfaces (eg Kiprijanoff 1881; Broili 1907; Kuhn 1946; McGowan 1972; Wade 1984; Murray 1987; Choo 1999). SAM P35431 also differs from the larger girdle elements of *Platypterygius* spp., in which the coracoid is subcircular in outline with dorsoventrally deep glenoid/intercoracoid facets (Broili 1907; Wade 1984), and both the scapula and ischiopubis are strap-like with predominantly narrow, ridge-like articular surfaces (Broili 1907; Nace 1939; Murray 1987).

SAM P35434 probably represents a juvenile individual because of its small size and poor ossification of the articular surfaces. Both it and SAM P35431 can be assigned to Plesiosauroidea on the basis of their anteroposteriorly short ventral plates. This differs from the condition in pliosauroids in which the ventral plate of the ischium bears a marked posterior expansion (Mehl 1912; Andrews 1913; Tarlo 1959, 1960; Brown 1981). The presence of a relatively weak posterior expansion in *Eurycleidus* (Cruikshank 1994) and *Leptocleidus* (pers. obs, AM F99374 from the Aptian–Albian Bulldog Shale of Coober Pedy, South Australia), however, suggests that this character state may not be universal for the group. SAM P35434 is unusual in its proportionately massive articular head relative to the ventral plate.

The phylogenetic significance of this feature, if any, is uncertain because of its immature stage of development.

ELASMOSAURIDAE Cope, 1869

Elasmosauridae gen. et sp. indet.

Material

SAM P35432 (Figs 5A, B, C, D), a single weathered posterior cervical vertebral centrum.

Locality

Casuarina Beach, north of Darwin, Northern Territory. Darwin Formation, Aptian or Albian.

Description

The surface of the centrum is badly weathered with very little periosteal bone remaining. Total length is 72.8 mm; width of anterior surface is 109.5 mm; depth of anterior surface is 85.2 mm. In general proportions, the centrum is anteroposteriorly short relative to both the height and width of the anterior articular surface. Both the lateral and ventral surfaces are shallowly concave, with the ventral surface being pierced by two large foramina. The articular surfaces are poorly preserved but clearly platycoelous, with a raised convex rim. The neural arch facets are indistinct but prominent bosses high on the lateral surface of the centrum indicate positioning of the rib facets.

Remarks

SAM P35432 is tentatively assigned to *Elasmosauridae* on the basis of its platycoelous articular surfaces. Murray (1987) reported an elasmosaurid cervical with very shallowly concave articular facets from the Casuarina Beach locality. Brown (1981, 1993) and Bardet et al. (1999) regarded the presence of platycoelous articular surfaces on the cervical centra to be a potential synapomorphy for *Elasmosauridae*. The character state has also been recorded in the Maastrichtian cryptoclidid *Morturneria* (Chatterjee & Small 1989), though Bardet et al. (1991) suggested that this taxon may represent a derived elasmosaurid.

The proportionately short centrum length relative to height of SAM P35432 differs from the common condition in elasmosaurids (such as that described by Murray 1987), in which the cervical centra are markedly elongate (Brown 1993; Bardet et al. 1999). The presence of relatively short cervical centra is considered plesiomorphic among

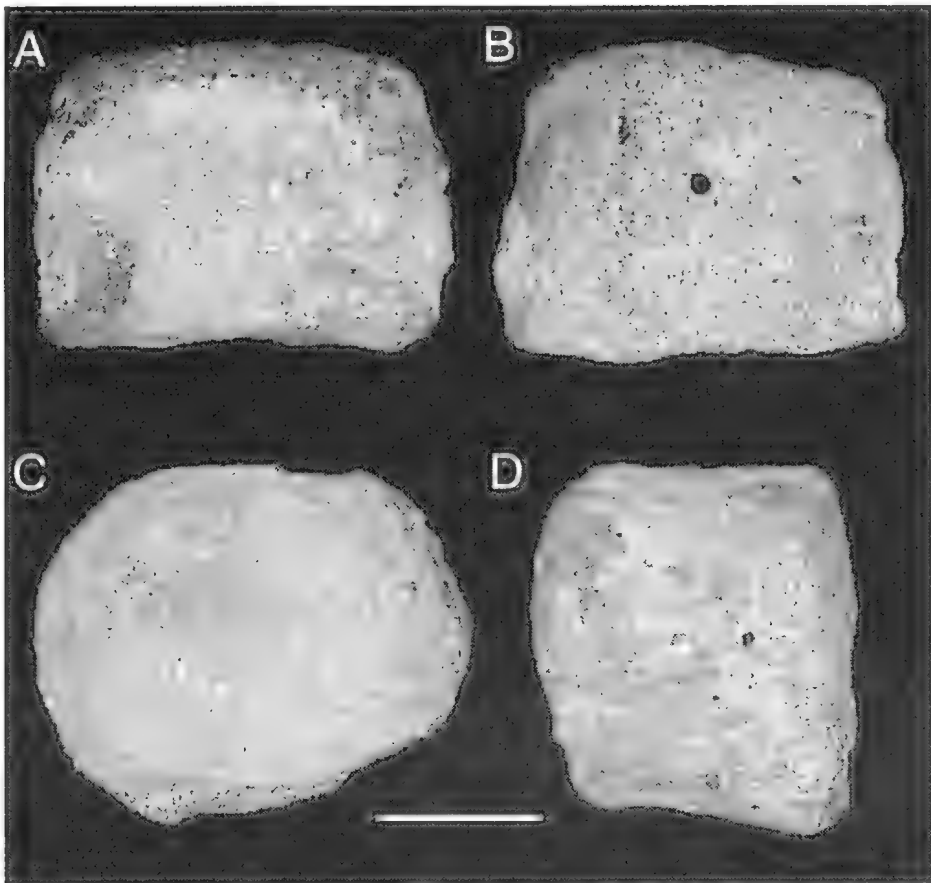


FIGURE 5. SAM P35432, Elasmosauridae gen. et sp. indet. posterior cervical centrum in (A) dorsal, (B) ventral, (C) anterior and (D) lateral views. Scale bar is 40 mm.

plesiosauroids (Brown 1993; Bardet *et al.* 1999). However, the feature has been described in the potential elasmosaurid taxa (*sensu* Bardet *et al.* 1991) *Aristonectes* (Cabrera 1941) and *Morturneria* (Chatterjee & Small 1989) as well as in indeterminate elasmosaurid posterior cervicals from unspecified (probably Albian) deposits near Oodnadatta (Freitag 1964) and the Neales River region (SAM P6181, Persson 1960), South Australia; Toolebuc Formation, Queensland (Kear 2001); and Molecap Greensand, Western Australia (Long & Cruickshank 1998). The presence of proportionately elongate cervicals may therefore not necessarily be universal amongst elasmosaurids, with some taxa exhibiting relatively short centra, particularly in the posterior cervical region.

SAM P35432 is notable for its possession of a raised convex rim surrounding the central

concavity of the articular surface. Brown *et al.* (1986) and Brown (1993) considered this a plesiomorphic condition commonly associated with members of the Cryptoclididae and Plesiosauridae. In contrast, elasmosaurids, including basal taxa such as *Occitanosaurus* (Bardet *et al.* 1999) and *Muraenosaurus* (Andrews 1910; Brown 1981, 1993), generally exhibit a more open V-shape, in which the articular surface margins form an abrupt angle with the centrum sides. A similar trait is evident in elasmosaurid material from the Toolebuc Formation of Queensland (Kear 2001), and is indicated (but not described) in the figured Darwin Formation specimen (NTM P8727-70, Fig. 1, p. 97) of Murray (1987). Carpenter (1996), however, considered articular rim morphology to be a variable character amongst plesiosaurs and of questionable diagnostic value.

PLIOSAUROIDEA Seeley, 1874

PLIOSAURIDAE Seeley, 1874

Leptocleidus Andrews, 1922

Leptocleidus sp.

Material

SAM P35053, cast of NTM P913-5 (Figs 6A, B, C) right femur.

Locality

Casuarina Beach, north of Darwin, Northern Territory. Darwin Formation, Aptian or Albian.

Description

A near complete right femur lacking part of posterodistal margin. Total length is 260.8 mm;

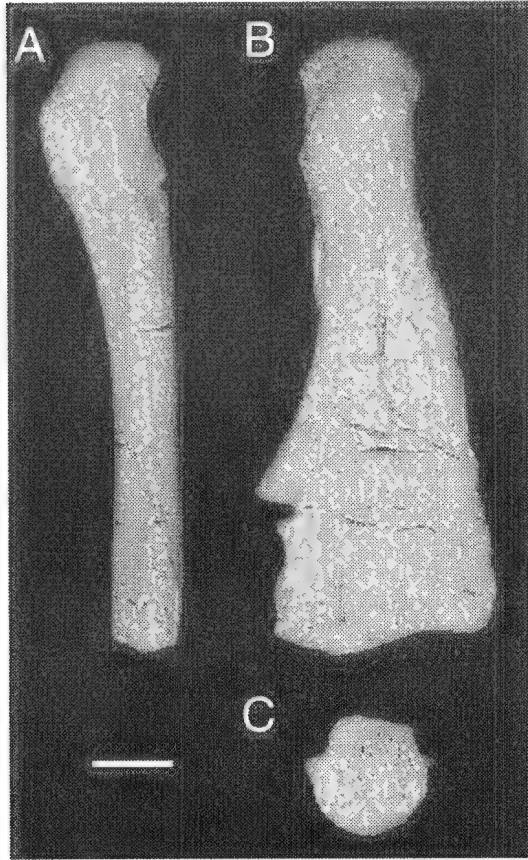


FIGURE 6. SAM P35053 (cast of NTM P913-5), *Leptocleidus* sp. femur in (A) anterior, (B) dorsal and (C) proximal views. Scale bar is 40 mm.

total proximal length is 47.9 mm; total proximal height (including trochanter) is 51.5 mm; width across base of dorsal trochanter is 37.2 mm; total distal length (not including missing posterior margin) is 91.6 mm; total distal height is 25.9 mm. The anterior edge of the femur is weakly sigmoidal, with a strongly convex distal extremity. The posterior edge is uniformly concave along its entire length. Both the dorsal and ventral surfaces are shallowly concave along their longitudinal axis; however, the ventral surface becomes convex and upturned towards the distal extremity. Proximally, the femur is greatly dorsoventrally expanded and separated from its distal section by a constricted neck. The dorsal trochanter is robust and anteroposteriorly constricted at its base. It is separated from the ovoid glenoid articular surface by a shallow groove. The surfaces of both the dorsal trochanter and glenoid articulation are deeply pitted, suggesting the presence of cartilage.

The femoral shaft is weakly anteroposteriorly constricted and ovoid in cross-section, with its posterior margin bearing a raised rugose tuberosity, possibly for attachment of the *m. caudifemoralis*. A second low tuberosity is present on the median ventral surface and may represent part of the *m. puboischiofemoralis* insertion. The distal femoral extremity is fan-shaped in dorsoventral outline, with a weakly projecting anterodistal margin. The distal articular surface is narrow and elliptical, with a raised median ridge separating the very large radial facet from the remains of the ulnar facet.

Remarks

Despite the poor existing knowledge of femoral morphology in *Leptocleidus* spp., SAM P35053 (NTM P913-5) can be readily distinguished from the proportionately shorter and stouter propodials of elasmosaurids (Brown 1981; Murray 1987) by its anteroposteriorly broad, flat femoral shaft, greatly expanded distal extremity and sigmoidal anterior margin. These characteristics are very similar to those of the fragmentary femora of *L. capensis* (Andrews 1911) and well-preserved material (AM F99374, SAM P15980) from the Bulldog Shale of South Australia (Figs 7A, B). The femur of *L. clemai* (Cruickshank & Long 1997) differs in its possession of a concave anterior margin. This feature, along with a proportionately more slender shaft, is also present in the femora of polycotyliids and most other pliosauroids (Andrews 1913; Welles 1943, 1962; Brown 1981; Storrs 1999). A sigmoidal anterior femoral and humeral margin has, however, been

TABLE 2. Marine reptile groups from Early Cretaceous deltaic-marine deposits of Australia. Pliosauroids are separated into small-bodied (eg *Leptocleidus*) and large-bodied (eg *Kronosaurus*) forms because of their differing ecological roles. The poorly known taxon '*Cimoliasaurus maccoyi*' is recorded separately because of its unknown affinity. Indeterminate plesiosaur material from the marine Bungil Formation, Queensland and freshwater deposits of the Griman Creek Formation, New South Wales, and Strzeleki and Otway Groups, Victoria is excluded pending a more thorough examination of the remains. Taxa from the opal bearing deposits of White Cliffs, New South Wales are placed within the Wallumbilla Formation in accordance with the lithostratigraphic nomenclature of Burton & Mason (1998). Source texts include: Etheridge (1904)¹, Longman (1924)², Tierchert & Matheson (1944)³, Persson (1960⁴, 1963⁵, 1982⁶), Ludbrook (1966)⁷, Condon (1968)⁸, Pledge (1980)⁹, Smart & Senior (1980)¹⁰, Gaffney (1981)¹¹, Molnar (1982¹², 1991¹³), Wade (1984¹⁴, 1990¹⁵), Murray (1985¹⁶, 1987¹⁷), Hocking et al. (1987)¹⁸, Burger (1988)¹⁹, Bardet (1992)²⁰, Thulborn & Turner (1993)²¹, Krieg & Rodgers (1995)²², Cruickshank & Long (1997)²³, Henderson (1998)²⁴, Long (1998)²⁵, Long & Cruickshank (1998)²⁶, Cruickshank et al. (1999)²⁷, Choo (1999)²⁸, Kear (2001)²⁹.

| Darwin Formation (Money Shoals Platform) Aptian/Albian | Wallumbilla Formation (Eromanga Basin) Aptian–Albian | Allaru Mudstone (Eromanga Basin) Albian | Toolebuc Formation (Eromanga Basin) Albian |
|--|---|---|---|
| Ichthyosauria ^{3,13,15,16,17} | Ichthyosauria ¹³ | Ichthyosauria ^{12,13,14,15,25} | Ichthyosauria ^{12,13,14,15,25} |
| Elasmosauridae ^{13,17} | Elasmosauridae ^{4,5,12,13,25} | Elasmosauridae ^{4,5,12,13,25} | Elasmosauridae ^{4,5,6,12,13,21,25,29} |
| Small pliosaurid ²⁷ | Large pliosaurid ^{1,2,4,5,12,13,21,25} Polycotylidae ^{4,5,13} ' <i>C. maccoyi</i> ' ^{1,4,13} | Chelonioidae ^{13,25} | Large pliosaurid ^{2,4,5,12,13} Polycotylidae ^{21,25,27} Chelonioidae ^{11,12,13,25} |
| Shallow near-shore marine ²⁴ / paralic ¹⁰ / possibly tidal ¹⁶ | Coastal / offshore shallow marine ^{10,19} | Shallow marine ¹⁰ | Shallow marine ¹⁰ |

cited as a potentially diagnostic character state for the polycotylid genus *Polycotylus* (Storrs 1999).

DISCUSSION

The Darwin Formation sediments have been interpreted as representing a shallow near-shore marine/paralic (Smart & Senior 1980; Henderson 1998) to possibly tidal (Murray 1985) depositional environment. The presence of the small pliosaurid taxon *Leptocleidus*, known elsewhere from freshwater and near-shore marine deposits (Andrews 1911, 1922; Strömer 1935; Cruickshank 1997; Cruickshank & Long 1997; Cruickshank et al. 1999), is consistent with this interpretation.

A comparison (Table 2) of the Darwin Formation marine reptile fauna with those known from Early Cretaceous deltaic-marine deposits elsewhere in Australia (Wallumbilla Formation [Doncaster Member], Allaru Mudstone, Toolebuc Formation and Mackunda Formation, Queensland; Bulldog Shale, South Australia; Wallumbilla Formation [Doncaster Member], New South Wales; Birdrong Sandstone and Barrow Group,

Western Australia) indicates greatest compositional similarity to the Hauterivian–Barremian Birdrong Sandstone fauna, with ichthyosaurs, elasmosaurids and the small-bodied pliosaurid *Leptocleidus* represented. Throughout the Early Cretaceous marine deposits, ichthyosaurs show a wide distribution (occurring in all currently recognised deposits except the Albian Mackunda Formation and unspecified Berriasian subsurface sediments of the Barrow Group), as do elasmosaurids, which have been recorded from all localities except those of the Albian Mackunda Formation and Berriasian Barrow Group.

Cruickshank et al. (1999) indicated the possible presence of cryptoclidids in the Aptian–Albian Bulldog Shale. This is supported by more recent observations of the South Australian fauna (Kear unpubl.) but as yet the group has not been recorded from any other Australian deposit.

The distribution of small- and large-bodied pliosaurid taxa in the Australian Early Cretaceous is variable, with smaller forms (represented by at least two species of *Leptocleidus*, Cruickshank et al. 1999) confined to the Darwin Formation,

TABLE 2. (cont.)

| Mackunda Formation (Eromanga Basin) Albian | Bulldog Shale (Eromanga Basin) Aptian–Albian | Birdrong Sandstone (Carnarvon Basin) Hauterivian–Barremian | Barrow Group (Carnarvon Basin) Berriasian |
|--|---|--|---|
| Polycotylidae ¹³ | Ichthyosauria ^{9,13,20} Elasmosauridae ^{9,27} Small pliosaurid ^{9,25,27} Large pliosaurid ⁹ Cryptoclididae? ²⁷ | Ichthyosauria ^{3,13,28} Elasmosauridae ^{26,27} Small pliosaurid ^{23,27} | Small pliosaurid ²⁶ |
| Paralic ¹⁰ | Shallow marine ²² / offshore ⁷ | Coastal near-shore shallow marine ¹⁸ / paralic ⁸ | Fluviatile-deltaic ¹⁸ |

Bulldog Shale and Birdrong Sandstone. Larger pliosaurid remains occur only in the Aptian–Albian Wallumbilla Formation (Doncaster Member), Albian Toolebuc Formation and Bulldog Shale deposits. This division may be linked to the different habitat preferences and ecological roles of small- and large-bodied pliosaurid taxa, with offshore environments preferentially supporting larger-bodied forms. An exception is seen in the shallow offshore marine (Ludbrook 1966; Krieg & Rogers 1995) Bulldog Shale, which includes both small- and large-bodied pliosaurid remains (the latter being represented by an isolated tooth, SAM P22525, from the opal-bearing sediments of Coober Pedy, figured by Pledge 1980, p. 8).

Distribution of polycotylids in the shallow marine (Smart & Senior 1980; Burger 1988) Wallumbilla Formation, Toolebuc Formation and paralic (Smart & Senior 1980) Mackunda Formation may, as with large-bodied pliosaurids, be related to a preference for predominantly offshore marine environments. However, individuals also appear to have readily

frequented more inshore habitats, as suggested by their occurrence in the Mackunda Formation deposits.

Restriction of chelonoids to the upper Albian Allaru Mudstone and Toolebuc Formation may be the product of both the group's temporal distribution (the earliest-known chelonoid being recorded from the upper Aptian – lower Albian Santana Formation of Brazil, Hirayama 1997, 1998) as well as environmental factors such as prevailing water temperatures. Studies of sedimentary sequences (Frakes & Francis 1988; Frakes & Krassay 1992; Frakes et al. 1995; Constantine et al. 1998), climatic modelling (Barron & Washington 1982) and isotope data (Gregory et al. 1989; Pirrie et al. 1995) have suggested that strongly seasonal climates with winter freezing and at least seasonal sea ice characterised high latitudes in the Early Cretaceous of Australia. Such conditions may well have been unfavourable to chelonoids and provided an effective barrier to the group's dispersal into the Australian region prior to the upper Albian.

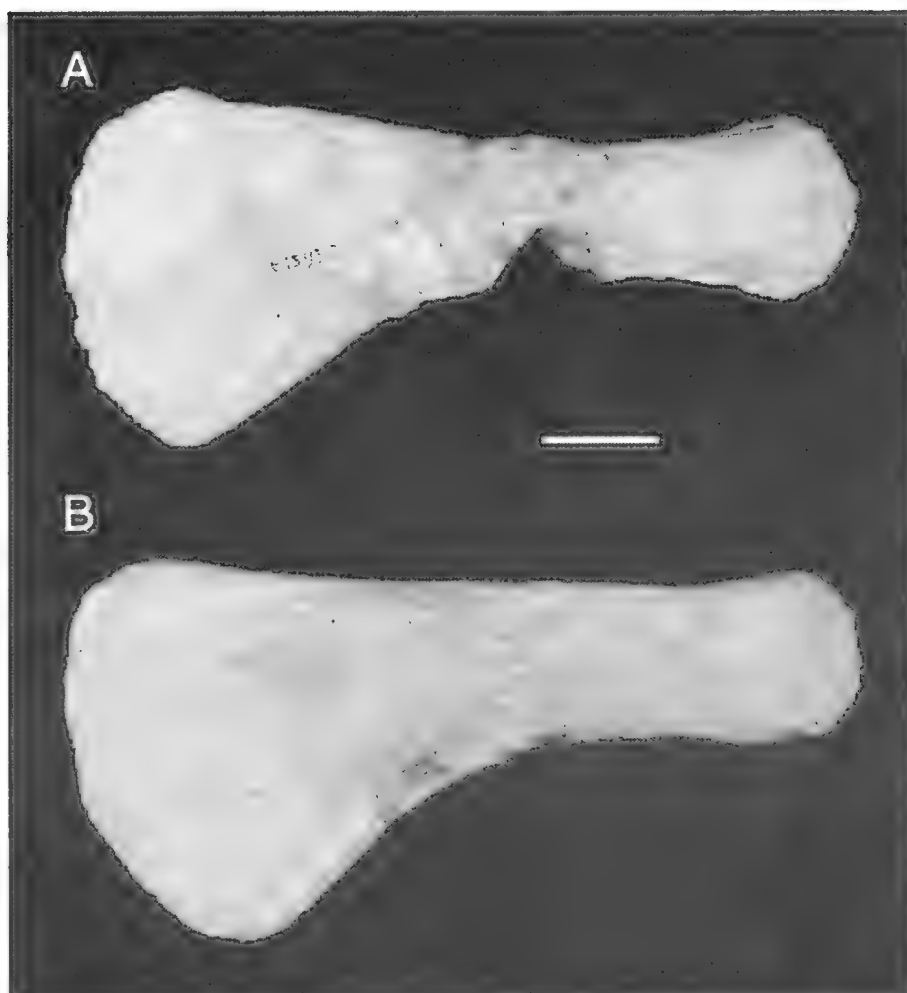


FIGURE 7. SAM P15980 juvenile *Leptocleidus* sp. humerus (A) and femur (B) from Andamooka, South Australia. Scale bar is 20 mm.

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